Toxodon

Toxodon (meaning "bow tooth" in reference to the curvature of the teeth) is an extinct genus of South American mammals from the Late Miocene to early Holocene epochs (Mayoan to Lujanian in the SALMA classification) (about 11.6 million to 11,000 years ago).[1][2] It is a member of Notoungulata, one of several now extinct orders of hoofed mammals indigenous to South America. It was among the largest and last members of its order, and was probably the most common large hoofed mammal in South America of its time.

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Taxonomy

Skeletal diagram

Toxodon was one of the last members of Notoungulata, a group of ungulates that had been part of the fauna of South America since the Paleocene. *Toxodon* was a member of Toxodontidae a large bodied group including similar, vaguely rhinoceros like forms.

Charles Darwin was one of the first to collect *Toxodon* fossils, after paying 18 pence for a *T. platensis* skull from a farmer in Uruguay.[3] In *The Voyage of the Beagle* Darwin wrote, "November 26th - I set out on my return in a direct line for Monte Video. Having heard of some giant's bones at a neighbouring farm-house on the Sarandis, a small stream entering the Rio Negro, I rode there accompanied by my host, and purchased for

Toxodon

Temporal range: Late Miocene-Holocene (Serravallian-Greenlandian)

11.6–0.011 Ma

Pre€ € O S D C P T J K PgN

Skeleton of *Toxodon* in Buenos Aires

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	†Notoungulata
Family:	†Toxodontidae
Subfamily:	†Toxodontinae
Genus:	†*Toxodon* Owen, 1837

Type species

†***Toxodon platensis***
Owen, 1837

Other species

- †*T. burmeisteri* Giebel, 1866
- †*T. chapalmalensis* Ameghino, 1908
- †*T. darwini* Burmeister, 1866

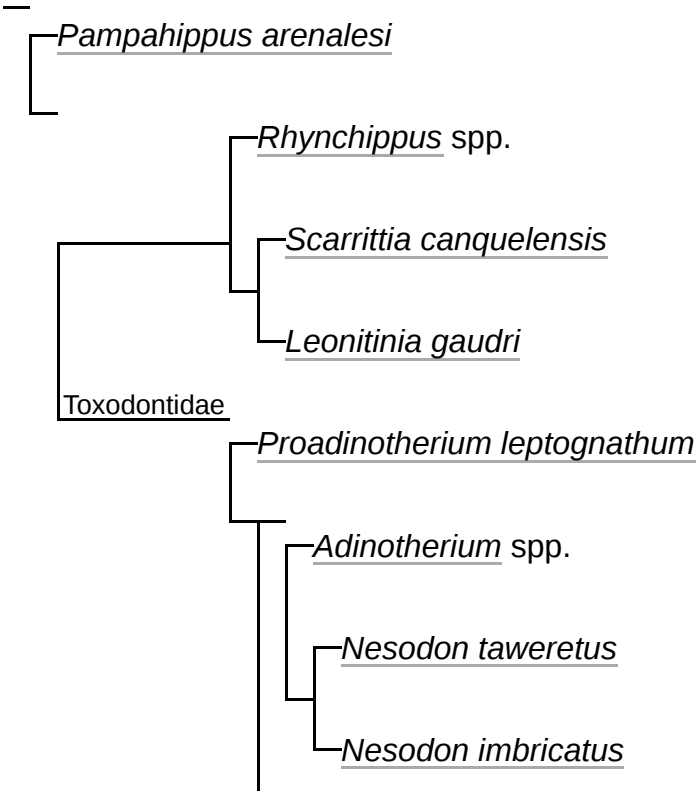
the value of eighteen pence the head of the *Toxodon*."[4] Since Darwin discovered that the fossils of similar mammals of South America were different from those in Europe, he invoked many debates about the evolution and natural selection of animals.

In his own words, Darwin wrote down in his journal, "*Lastly, the Toxodon, perhaps one of the strangest animals ever discovered: in size it equaled an elephant or megatherium, but the structure of its teeth, as Mr. Owen states, proves indisputably that it was intimately related to the Gnawers, the order which, at the present day, includes most of the smallest quadrupeds: in many details it is allied to the Pachydermata: judging from the position of its eyes, ears, and nostrils, it was probably aquatic, like the Dugong and Manatee, to which it is also allied. How wonderfully are the different Orders, at the present time so well separated, blended together in different points of the structure of the Toxodon!*"

Analysis of collagen sequences obtained from *Toxodon* as well as from *Macrauchenia* found that South America's native notoungulates and litopterns form a sister group to perissodactyls, making them true ungulates.[5][6] This finding has been corroborated by an analysis of mitochondrial DNA extracted from a *Macrauchenia* fossil, which yielded a date of 66 Ma for the time of the split with perissodactyls.[7]

Evolution

In 2014, a study identifying a new species of toxodontid resolved the phylogenetic relations of the toxodontids, including to *Toxodon*. The below cladogram was found by the study:[8]



- †*T. ensenadensis* Ameghino, 1887
- †*T. expansidens* Cope, 1886
- †*T. gracilis* Gervais and Ameghino, 1880

Synonyms

Genus-level

- *Dilobodon* Ameghino, 1886
- *Chapalmalodon* Pascual, 1957
- *Chapadmalodon* Tonni *et al.*, 1992 (lapsus calami)

T. platensis

- *T. angustidens* Owen, 1846
- *T. owenii* Burmeister, 1866
- *T. gervaisii* Gervais & Ameghino, 1880
- *T. aguirrei* Ameghino, 1917
- *T. gezi* Ameghino, 1917

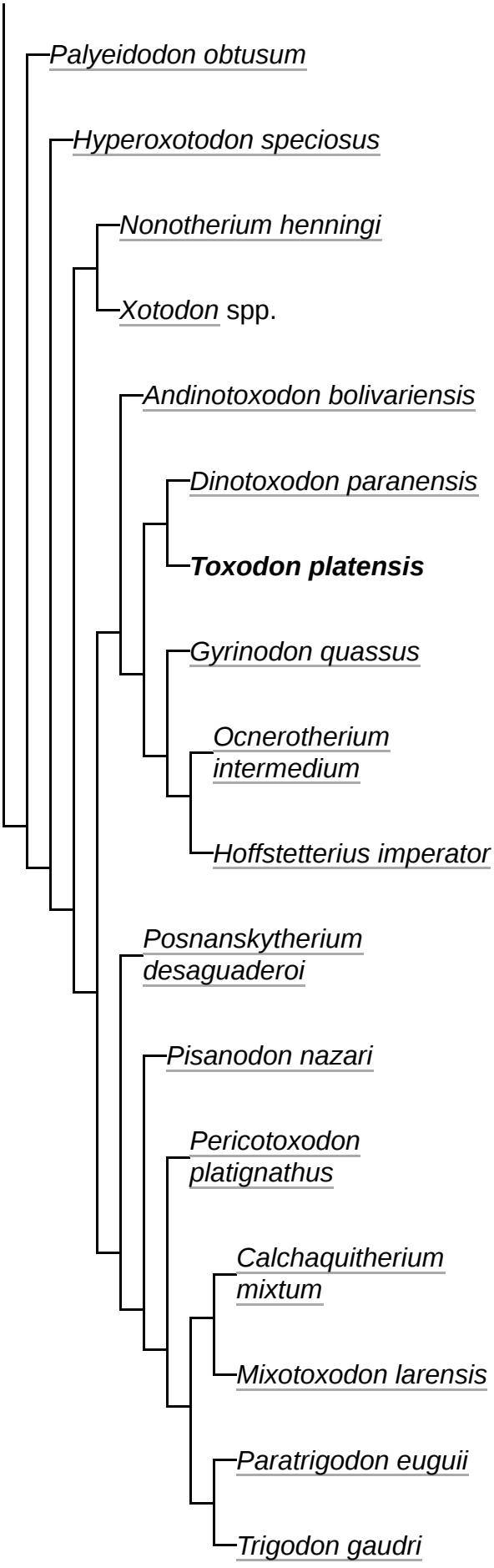
T. burmeisteri

- *T. paradoxus* Ameghino, 1882
- *T. protoburmeisteri* Ameghino, 1887
- *T. bilobidens* Ameghino, 1887

T. chapalmalensis

- *Chapalmalodon chapalmalensis* Pascual, 1957
- *T. chapadmalensis* Cione & Tonni, 1995 (lapsus calami)
- *T. chapalmalalensis* Oliva & Cerdeno, 2007 (lapsus calami)

T. ensenadensis



- *T. giganteus* Moreno, 1888
- *T. elongatus* Roth, 1898

T. gracilis

- *T. voghti* Moreno, 1888

Description

Toxodon was about 2.7 m (8 ft 10 in) in body length, with an estimated weight up to 1,415 kg (3,120 lb)[9] and about 1.5 m (4 ft 11 in) high at the shoulder and resembled a heavy rhinoceros, with a short and vaguely hippopotamus-like head.[10] Because of the position of its nasal openings, it is believed that *Toxodon* had a well-developed snout. *Toxodon* possessed a large, barrel shaped body.[11] It had short stout legs with plantigrade feet with three functional relatively short toes.[11] The hind limbs are longer and raised higher than the front limbs, giving a sloped appearance to the body.[11] Like horses, it had a stay apparatus allowing the knees to be passively locked while standing.[12]

The vertebrae were equipped with high apophyses, which most likely supported the massive weight and muscles as well as its powerful head. *Toxodon* had broad jaws which were filled with bow shaped teeth and incisors.[13] The teeth of *Toxodon* have no roots and are ever-growing (euhypsodont) like those of rodents and lagomorphs, and often exhibit enamel hypoplasia.[14]

Palaeobiology

Toxodon skull in front view

It was initially believed to have been amphibious, but after examining the proportions of the femur and tibia, as well as the position of its head, below the top of the spinal column, palaeontologists realized that it had features similar to terrestrial animals such as elephants or rhinoceroses. The fossils are also usually found in arid and semi-arid areas, typically an indication of a primarily terrestrial life.

Toxodon would have had a very unusual gait, due to its peculiar proportions. It may have galloped to escape predators, but like a rhino, it probably relied more on its size as protection against predators.

Toxodon is believed to have been ecologically plastic, with its diet varying according to local conditions,[15] with an almost totally C_3 browsing diet in the Amazon rainforest, mixed feeding C_3 in Bahia and the Pampas to almost completely C_4 dominated grazing diet in the Chaco.[16]

Extinction

Toxodon became extinct at the beginning of the Holocene as part of the Quaternary extinction event, alongside almost all other large animals in South America. Previous mid-Holocene dates are now thought to be in error.[17]

Distribution

Toxodon has a wide distribution in South America during the Late Pleistocene, extending from the Pampas into the Amazon rainforest.

Fossils of *Toxodon* have been found in:[2][18]

Holocene

- Abismo Ponto de Flecha, Brazil

Pleistocene

- San José, Fortin Tres Pozos, Chaco and Luján Formations, Argentina
- Tarija and Ñuapua Formations, Bolivia
- Brazil
- Guatemala
- Panama
- Paraguay
- Sopas and Dolores Formations, Uruguay

Miocene-Pliocene (Montehermosan)

- Monte Hermoso Formation, Argentina

Miocene

- Ituzaingó Formation, then described as Entrerriana Formation, Argentina

Restoration of *T. platensis*

Toxodon skull, Zoologisk Museum, Copenhagen

Restoration of *Toxodon platensis*

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